How Similar are Geographically Separated Stands of the Same Vegetation Formation? A Moorland Example from Tasmania and Mainland Australia.

DAVID KEITH

KEITH, D. A. How similar are geographically separated stands of the same vegetation formation? A moorland example from Tasmania and mainland Australia. Proc. Linn. Soc. N.S. W. 115: 61-75 (1995).

Broad-scale, intuitively derived vegetation maps and classifications are used for a variety of purposes including evaluation of representativeness and determination of priorities in conservation planning. Such uses assume that stands of vegetation ascribed to particular units of classification or map share characteristics (e.g. composition, structure) that differentiate them from stands ascribed to other units. To test this, moorland vegetation was compared at two widely separated locations that have been included within one vegetation unit by several authors. Vegetation at the two locations had similar structure and similar compositional gradients, though some statistically significant differences were demonstrated. There were major differences in floristic composition and richness, overall habitat characteristics and the responses of individual species to a soil gradient. For example, there were more species in common between moorland and woodland in the same area than between moorlands at different locations. The results highlight the limitations of using broad-scale, intuitively defined units of mapping and classification of conservation planning. Alternative approaches include regional partitioning of units or description of vegetation at finer scales, depending on the nature of heterogeneity within units.

D. A. Keith, New South Wales National Parks and Wildlife Service, P.O. Box 1967, Hurstville, Australia 2220; manuscript received 24 April 1994, accepted 21 September 1994.

KEYWORDS: Biogeography, classification, conservation planning, gradient response, map units, mire, realised niche.

INTRODUCTION

In recent decades vegetation has been classified and mapped over large parts of the world's land surface (e.g. Kuchler, 1964; Sochava and Lukicheva, 1964; Carnahan, 1976; White, 1983). Australian examples that cover broad areas at small scales include the work of Beard and Webb (1974), Specht *et al.* (1974), Carnahan (1976), Beadle (1981), Kirkpatrick and Dickinson (1983), Baur (1988), Resource Assessment Commission (1992) and Pickard (1994). Units of classification and mapping are defined in terms of physiognomy, structure, floristics of the dominant stratum and/or environmental features, usually intuitively or according to some pre-determined framework.

These maps and classifications are used extensively in resource economics, landscape geography, comparative ecology and conservation planning. An important assumption that underpins such uses is that the units of classification and mapping delineate stands of vegetation which share features in common that distinguish them from stands ascribed to other units. In conservation planning, for example, a vegetation map is expected to identify areas with similar habitat characteristics, structure and species composition, from which a representative sample may be selected for reservation (Austin and Margules, 1986). How reliably do small-scale maps and classifications fulfil this need? There is insufficient knowledge of the variability within units of classification and mapping to understand the limitations of these widely used tools.

Another aspect of variability within units of classification and mapping concerns

genetic variation and the role of species within ecosystems. Genetic and ecosystem components of biodiversity are poorly understood, relative to species diversity, even though their significance for conservation is now widely accepted (WRI, IUCN and UNEP, 1992). Comparative studies of vegetation can elucidate patterns in these components of biodiversity indirectly, as illustrated by Hutchinson's (1959) notion of the realised niche. Niche differentiation between populations of the same species at separate locations may represent variability derived from genetic or ecosystem components of diversity. An understanding of such patterns will contribute to the assessment of maps and classifications for conservation planning.

Very few studies have examined properties of map units at local and regional scales (e.g. Burgman, 1988; Pressey and Bedward, 1991). Similarly, few studies have addressed the occurrence of species in relation to interactions between their responses to different environmental factors (e.g. Austin *et al.* 1983). Quantitative comparisons of vegetation units and their component species between areas separated by large distances are apparently non-existent. In this paper, the following characteristics of moorland vegetation were compared at two widely separated locations in south-eastern Australia: (1) overall floristic composition; (2) vegetation structure and species richness; (3) overall characteristics of the habitat (climate, landscape and soils); (4) variation in floristic composition in relation to local environmental gradients; and (5) gradient responses of species common to both locations.

Methods

Study Areas

Moorland is a very distinctive type of treeless vegetation found in waterlogged soils at low to moderate elevation from south-east Queensland to southern Tasmania. In the Bulli area, south of Sydney (34°14'S 150°54'E, Fig. 1) moorland occurs on a Hawkesbury Sandstone plateau, 300-400 m above sea level. Vegetation of the area was described by Davis (1941), Keith and Myerscough (1993) and Keith (1994a). In the Melaleuca area (also known as New Harbour district) in south-west Tasmania (43° 26'S 146°09'E, Fig. 1), moorland occurs on a peneplain and surrounding quartzite hills, from sea level to well over 400 m. Vegetation was described by Davis (1940) and Keith and Pellow (1989). A similar area of moorland was sampled at each location (3400ha at Bulli, 3100ha at Melaleuca).

Similarities between these moorlands were first described by Davis (1940, 1941). Recognising a conspicuous dominant at both locations, Davis described each moorland as a *Gymnoschoenus sphaerocephalus* community. This view was subsequently taken up by Specht *et al.* (1974) who listed alliances dominated by *G. sphaerocephalus* for the central coast of N.S.W. and south-west Tasmania, and by Beadle (1981) who considered two intergrading alliances, one dominated by *G. sphaerocephalus* and the other dominated by *Calorophus minor (=Empodisma minus)* and *Leptocarpus tenax*. Carnahan (1976) mapped the area around Melaleuca as gG3, a tussock grassland dominated by Cyperaccae, and it is likely that he would have classified the moorlands at Bulli similarly, but these cover areas too small to map at 1:6,000,000 scale.

While each of these authors clearly recognized geographic variation within their respective units of classification, they emphasised similarities in structure, floristics and environment over the broad distributional range of the units. Describing the Bulli moorlands Davis (1941) wrote, "The community is exactly similar to the extensive Button-grass Plains of Tasmania [Melaleuca]... The structure is identical, and the most prominent species (*G. sphaerocephalus*) is common to both. Many of the subsidiary species are common to both expressions of the community, though the Tasmanian development is, as



Fig. 1. Map of south-eastern Australia showing location of Bulli and Melaleuca study areas and the distribution of moorland vegetation.

would be expected, richer florisitically, than the present example [Bulli] being extralimital."

Data collection

Vascular plant taxa were scored as present or absent in contiguous 0.5 x 0.5 m quadrats along 30 m transects. The abundance of each taxon at each transect was expressed as the proportion of quadrats occupied. The location of the 60 transects recorded at Bulli was stratified according to 7 classes based on soil drainage and vegetation structure (Keith and Myerscough, 1993). Due to time constraints, only 30 transects were recorded at Melaleuca, their location stratified by classes based on soil drainage and topography (Keith and Pellow, 1990).

The height and cover of shrub and herbaceous strata were estimated at 5-metre intervals along each transect and mean values were calculated for each transect. Ten soil cores, 2 cm diameter x 7 cm depth, were sampled at regular intervals along transects and homogenised. Soils were analysed for pH, organic matter content (loss on ignition), exchangeable Na, K, Ca, Mg and Al, and total (acid soluble) P.

Mean monthly minimum and maximum temperature data and mean monthly rainfall data were obtained from the Australian Bureau of Meteorology for stations in each study area (Melaleuca and Maddens Plains). No temperature data were available within the Bulli study area, so data were obtained for a station at Lucas Heights (150 m elevation), 22 km to the north.

DATA ANALYSIS

Overall floristic composition

Similarity in overall floristic composition was examined by simple tabulation and ordination. Taxa were assigned to one of the following groups: represented only at Bulli; only at Melaleuca; or common to both localities. The proportion of moorland taxa at Bulli also represented in moorland at Melaleuca was compared with the proportion represented in a nearby woodland community at Bulli (Keith 1994a) using the *z* test (Snedecor and Cochran 1963). An ordination was carried out on the transect data from both locations. An association matrix was calculated from the combined data matrix using the Kulzcynski coefficient (Faith *et al.*, 1987). Configurations were fitted in 2, 3 and 4 dimensions using a global non-metric multidimensional scaling algorithm (Minchin 1990) according to the procedure described by Keith (1994a).

Vegetation structure and species richness

To provide a framework for comparison of vegetation structure and species richness, separate classifications were performed on floristic data from each location. An unweighted pair-group arithmetic averaging (UPGMA) clustering procedure was applied to association matrices calculated using the Kulzcynski coefficient (Belbin, 1986). Floristic groups were defined in each dendrogram using the procedure described by Keith and Myerscough (1993). Each floristic group was characterised by its topographic position in the landscape: along drainage lines; on lower slopes and seepage zones; or on drier upper slopes. Floristic groups were defined as analogous between the two locations if they occupied the same topographic position. Mean height and cover of shrub and herbaceous strata and mean species richness for 15 m² were compared between analogous floristic groups using t tests (Snedecor and Cochran, 1963).

Habitat characteristics

Climatic variables were compared between locations graphically. Landscapes were compared by examination of aerial photographs to determine the proportion of area and

types of landform occupied by moorland at each location. Soils were compared by tabulating the total ranges of soil variables at each location.

Environmental Gradients

To examine the relationship between floristic composition and local gradients in soil properties, ordinations were derived for each of the two locations. Ordinations were performed on floristic data using the Kulzcynski coefficient and multidimensional scaling, as previously described. Vectors for each soil variable were fitted to floristic ordinations using a least squares method and a Monte-Carlo procedure to test the significance of correlations (Minchin 1990).

Gradient Responses

Gradient responses were compared between locations in a set of 13 species that were abundant at both locations. Five classes of soil phosphorus content, containing roughly equal numbers of samples at each location were defined: <90; 91-139; 140-185; 186-250; and >250 ppm. Differences in species' response to the phosphorus gradient between the two localities were tested using an analysis of deviance by fitting logit-linear models, assuming a binomial error distribution (McCullagh and Nelder 1983). Models were of the form $\mu = \beta_0 + \beta_1 . P + \beta_2 . L + \beta_3 (P.L)$, where μ is the proportion of quadrats in a transect occupied by the species, β_0 is the binomial error term, with the number of quadrats per transect as its denominator, P is the soil phosphorus class (1-5), L is the location (Bulli or Melaleuca), P.L is the interaction term and β_1 , β_2 and β_3 are coefficients for P, L and P.L, respectively. Differences in gradient response were tested using a stepwise modelling procedure. First the null model was fitted, then the full model was added, then the interaction term was eliminated from the full model. The statistical significance of the change in deviance associated with elimination of the interaction term was assessed in relation to the chi-squared distribution (McCullagh and Nelder, 1983).

RESULTS

Overall floristic composition

At the species level, only 12% of the combined moorland flora was common to both regions (Table 1). However, floristic differences diminish at higher taxonomic levels, with 36% of genera and 62% of families held in common. Shared taxa were spread evenly amongst growth forms, except that ferns are proportionately more represented. Taxa not represented in both floras fall into several categories: (i) local endemics (e.g. *Isophysis tasmanica* at Melaleuca, *Pultenaea aristata* at Bulli); (ii) relatively widespread taxa whose range does not extend to one of the localities (e.g. *Leptospermum scoparium* at Melaleuca, *Banksia robur* at Bulli); (iii) taxa represented in both localities, but only in moorland habitats at one (e.g. *Banksia marginata* and *Bauera rubioides* in moorland at Melaleuca, but only in woodland at Bulli); and (iv) itinerant taxa from adjacent habitats (e.g. *Anodopetalum biglandulosum* common in adjacent rainforest at Melaleuca, *Acacia terminalis* common in adjacent woodland at Bulli).

Of 167 vascular taxa present in the Bulli moorlands, 55 (33%) were recorded in a nearby woodland community (Sandstone Woodland of Keith 1994a), compared with 29 (17%) recorded in Melaleuca moorlands, a significantly different proportion (z=3.31, P<0.01).

Stress values for ordinations in 2, 3 and 4 dimensions were 0.1238, 0.0883 and 0.0761, respectively. Inspection of scatter plots indicated that the configuration of points on the first two axes was similar in all ordinations. Therefore the results of the 2-dimensional ordination were presented. Separation of samples along the first ordination axis shows that major differences in florisitic composition were related to geographic separa-

TABLE 1: Moorland floras of Bulli (NSW) and Melaleuca (Tas). Taxon Both Melaleuca Bulli Total Regions Only Only 29(12%) 74(31%) 138(57%) 241 Species 127 Genus 46(36%) 27(21%)54(43%) Family 33(62%) 7(13%) 13(25%) 53

tion of the two locations (Fig. 2). However, in each of the two clusters there is a parallel arrangement of samples along the second axes, suggesting a common environmental trend in floristics.

Vegetation structure and species richness

The cluster analyses allowed recognition of 5 floristic groups at Bulli (after Keith and Myerscough 1993): Ti-tree Thicket (TT); Cyperoid Heath (CH); Sedgeland (SL); Restioid Heath (RH); and Banksia Thicket (BT), and 4 groups at Melaleuca (nomenclature follows Jarman *et al.* 1988): Creek Copse (CC); Layered Blanket Moor (LB); Standard Peat (SP); and Alkaline Pan (AP). Fig. 3 shows floristic relationships among groups at each locality. TT and CC were considered analogous because both were thicket occurring along drainage lines. CH and LB were considered analogous because both were dense heath occurring in seepage zones. SL, RH and SP were considered analogous because all were open sedgeland-heath occurring on drier slopes. BT, a thicket on drier slopes at



Fig. 2. Ordination based on floristic composition of 60 samples from Bulli (open squares) and 30 samples from Melaleuca (closed circles).



Fig. 3. Dendrograms showing relationships between floristic groups based on separate analyses of data from each of Bulli and Melaleuca. S, se and n give the mean species richness per 15 m^2 , standard error and number of samples for respective floristic groups.

Bulli had no analogue at Melaleuca. AP, a heath community on flats subject to occasional tidal flooding at Melaleuca had no analogue at Bulli.

All floristic groups at Bulli were significantly richer in species at 15 m² scale than their analogues at Melaleuca (Fig. 3, P<0.001). Thickets along drainage lines had a taller and denser shrub stratum at Melaleuca (CC) than at Bulli (TT), and their ground stratum was denser at Bulli, but not different in height (Fig 4). At Bulli, dense heath in seepage zones had slightly less shrub cover and a slightly taller ground stratum than at Melaleuca, but otherwise there were no differences (Fig. 5). The structure of open sedgeland-heath on drier slopes at both locations was also similar. Both strata were slightly taller at Bulli than at Melaleuca, while cover did not differ, except that ground cover was greater in Restioid Heath than in Standard Peat (Fig. 6).

Habitat Characteristics

Mean monthly temperatures were 3-7°C greater at Lucas Heights (*cf.* Bulli) than at Melaleuca (Fig. 7). The greatest differences in temperatures occurred in summer. Mean annual rainfall is almost 700mm greater at Melaleuca than at Maddens Plains (Bulli) (Fig. 8). At Melaleuca, maximum rainfall occurs in winter months, while Maddens Plains experiences peak rainfall in summer.

At Bulli, moorlands occupied approximately 15% of the landscape, the remainder being occupied by dry sclerophyll woodland and forest. Moorlands at Bulli were restricted to gently sloping headwater valleys, the interfluves and steeper gullies were invariably occupied by woodland and forest respectively. At Melaleuca, moorlands occupied approximately 85% of the landscape, the remainder being occupied by wet sclerophyll forest and rainforest. Moorland at Melaleuca was widespread on flats, steep slopes and summits, while forest was restricted to the most sheltered sites.

Site 19 at Melaleuca (Alkaline Pan) was excluded from soil comparisons because tidal influence resulted in extreme values of some soil constituents, particularly exchangeable Na. Soil pH was similar at Melaleuca and Bulli, though soils were slightly less acidic at Bulli (Table 2). Moorland soil contained more organic matter at Melaleuca than at Bulli, though values overlap (Table 2). Levels of total soil phosphorus were similar at the two locations, but varied over a wider range at Melaleuca than at Bulli (Table 2). Exchangeable cations were, overall, more abundant in Melaleuca soils, however differences varied between cations. Levels of exchangeable Ca and Mg were much higher at Melaleuca than Bulli, while exchangeable Na and K were slightly higher. Levels of

exchangeable aluminium were much higher at Bulli than at Melaleuca (Table 2).

	Bulli	Melaleuca	
Soil Property			
pH	3.4-4.1	3.1-3.8	
Exchangeable Na	0.04 - 1.41	0.36 - 2.47	
Exchangeable K	0.10-0.75	0.13 - 1.24	
Exchangeable Ca	0.10 - 1.50	0.10-5.70	
Exchangeable Mg	0.10-2.20	1.40 - 12.70	
Exchangeable Al	0.04-6.00	0.04-0.90	
Total Exch. Cations	0.38 - 12.46	2.44-21.51	
Organic matter	0.2 - 43.6	10.2 - 69.1	
Total P	60 - 290	20 - 350	

Variation in soil properties of moorland soils at Bulli (NSW) and Melaleuca (Tas). Exchangeable cations in milliequivalents per 100 g air-dried soil. Organic matter is % air-dry mass. Total phosphorus is ppm acid-soluble phosphorus in air-dried soil.

TABLE 2:

TABLE 3:

Correlations between floristic ordination vectors and soil properties at Bulli (NSW) and Melaleuca (Tas).

Soil Property		Bulli	Bulli		Melaleuca	
	n	R	Р	n	R	Р
pH	18	.3642	.741	29	.6153	.028*
Exchangeable Na	18	.8395	.002**	29	.7218	.002**
Exchangeable K	18	.7894	.004**	29	.7048	.006**
Exchangeable Ca	18	.6895	.048*	29	.7400	.004**
Exchangeable Mg	18	.8252	.004**	29	.7391	.002**
Exchangeable Al	18	.9515	.000***	29	.7615	.000***
Total cations	18	.9198	.000***	29	.7528	.000***
Organic matter	18	.9140	.000***	29	.5811	.026*
Total P	18	.9133	.000***	29	.6023	.026*

Environmental Gradients

For the Bulli floristic data, stress values for ordinations in 2, 3 and 4 dimensions were 0.1453, 0.1026 and 0.0821, respectively, while for the Melaleuca data they were 0.1229, 0.0845 and 0.0568, respectively. Correlations for vectors fitted in 4 dimensions are shown in Table 3, those for vectors fitted in 3 dimensions were similar. At both locations total exchangeable cations and exchangeable Al were highly correlated with floristic composition and there were strong correlations with exchangeable Na, K and Mg. Correlations between floristic composition and exchangeable Ca and pH were stronger at Melaleuca than at Bulli. Total phosphorus and organic matter were much more highly correlated with floristic composition at Bulli than at Melaleuca.

Gradient Responses

There was a significant interaction between soil phosphorus and location in the distributional models for 12 out of the 13 species examined (Table 4). Thus, with the exception of *Lepidosperma filforme*, a species' response to the soil phosphorus gradient varied with location. The full models accounted for between 27 and 85% of the total deviance in the null model (Table 4), suggesting that factors other than soil phosphorus and location influence abundance, at least in some species. There were not sufficient data to examine other factors.



Fig 4: Mean height (a) and cover (b) with standard errors for each of shrub and ground strata in thicket along drainage lines at Bulli (open bars) and Melaleuca (solid bars).



Fig 5: Mean height (a) and cover (b) with standard errors for each of shrub and ground strata in dense heath in seepage zones at Bulli (open bars) and Melaleuca (solid bars).



Fig 6: Mean height (a) and cover (b) with standard errors for each of shrub and ground strata in open sedgelandheath on drier slopes at Bulli (open and hatched bars) and Melaleuca (solid bars).



Fig 7: Mean monthly minimum and maximum temperatures for Lucas Heights near Bulli study area (unbroken line) and Melaleuca (broken line).



Fig 8: Mean monthly precipitation for Maddens Plains in Bulli study area (open bars, mean annual total 1546 mm) and Melaleuca (solid bars, mean annual total 2212 mm).

DISCUSSION

Similarities and differences

Similarities between the geographically separated moorlands were limited. Of all the characteristics examined, there was greatest convergence in vegetation structure. Although there were a number of statistically significant differences in height and cover of various components, these differences were generally small in magnitude (Figs. 4-6). Some of these structural differences may relate to differences in fire history. Floristic similarities were limited, contrary to the remarks of Davis (1941), although some of the small number of shared species were visually conspicuous (e.g. *Gymnoschoenus sphaerocephalus, Melaleuca squarrosa*). The pattern of shared taxa reflects in part the intermittent isolation of Tasmania from the Australian mainland as a consequence of climatic fluctuation during the past million years (Barlow, 1981). Neither do the data support Davis' (1941) contention that Melaleuca moorlands are floristically richer than those at Bulli. In fact, the reverse is true, even though Australian moorlands reach their greatest spatial development in Tasmania (Jarman *et al.*, 1988).

There were substantial differences in climate, landscape and some soil characteristics between moorlands at the two locations. Nonetheless, ordination of combined data suggests that there may be analogous floristic trends in relation to a local environmental gradient (Fig. 2). Correlations between floristic vectors and certain soil variables at both locations (Table 3) support this interpretation. The apparent commonality of gradients may reflect similarity in processes that influence the distribution and abundance of plant species at each locality. Dynamic soil gradients and recurring fires have both been implicated as driving forces in vegetation dynamics of moorlands and heathlands in Tasmania (Jackson, 1968; Brown and Podger, 1982; Bowman *et al.*, 1986) and the central coast of New South Wales (Siddiqi *et al.* 1976a,b; Keith 1991; Keith 1994b, Keith and Bradstock 1994). While differences in gradient responses between species within regions have previously been reported (e.g. Austin *et al.*, 1983), the possibility that differences may exist within species between regions has received little attention from community ecologists. Even though similar environmental gradients appear to regulate the composition of vegetation at Bulli and Melaleuca, the response of any given species to these gradients may not be the same at different locations (Table 4). The statistical analyses are supported by the observation that some other species are represented exclusively in different habitats at each location (e.g. *Banksia marginata, Bauera rubioides*). There may be several explanations for such phenomena: genetic variability within species that affect their physiological range of tolerance (e.g. Hamerick 1983); physiological interactions within plants such that the level of one resource factor affects utilisation or tolerance of another (Tilman 1982); and ecological interactions between species such that a species' local distribution and abundance depends on the presence or absence of its competitors and predators (Connell 1975).

		Р						
Model: Degrees of freedom:	Null 51	+P+L+P.L 9	-P.L 5					
Boronia parviflora	703.3	314.8	70.6	<0.001				
Cassytha glabella	806.2	420.0	39.4	< 0.001				
Drosera binata	506.4	138.6	79.7	< 0.001				
Empodisma minus	1068.7	296.0	117.7	< 0.001				
Epacris obtusifolia	842.7	277.3	17.6	< 0.01				
Gymnoschoenus sphaerocephalus	1057.6	695.4	15.0	< 0.01				
Lepidosperma filiforme	663.8	561.1	7.9	ns				
Leptocarpus tenax	1157.0	615.6	100.1	< 0.001				
Lycopodium laterale	574.0	266.4	47.8	< 0.001				
Restio complanatus	1020.5	352.1	56.3	< 0.001				
Selaginella uliginosa	601.0	292.1	52.6	< 0.001				
Sprengelia incarnata	1334.2	728.9	116.3	< 0.001				
Xyris operculata	1092.8	339.2	44.6	< 0.001				

 TABLE 4:

 Logit-linear models of species occurrence in relation to soil phosphorus (P) and location (L).

 Right-hand column indicates significance of interaction term (P.L).

Implications for use of small-scale maps and classifications

The high level of variability in moorland vegetation and its environment between, relative to within, the two locations examined in this study highlights the limitations of using intuitively defined, broad-scale classifications and maps in conservation assessments. The accuracy of such assessments depends on the extent to which representation of classification units in reserves reflects representation of species and their assemblages, since these are the primary objects of conservation goals. The strength of this relationship, in turn, depends on heterogeneity within classification units, which is inversely related to scale (Bedward *et al.*, 1992). The intuitive method by which broad-scale units of classification and map are defined also reflects upon their reliability, although this effect is difficult to quantify because of its subjective nature.

The results for geographically separated moorlands show that similarities in vegetation structure and shared occurrences of conspicuous species do not necessarily reflect similarities in other features of vegetation, most notably overall floristic composition. The reliability of units of classification and mapping defined on this basis is therefore limited for certain uses.

Several studies in Australia have attempted to assess conservation needs and priorities using intuitively defined, broad-scale classifications (e.g. Specht et al., 1974; Benson, 1989; Resource Assessment Commission, 1992). The moorland example suggests that such assessments should be used cautiously. A high proportion of the total moorland in Australia could be reserved in the southern part of its range, but many moorland species and gradient patterns would not be represented unless reserves also sampled other parts of moorland distribution. Indeed, the results of the floristic analyses suggest that better representation might be achieved if Bulli moorland and woodland were lumped together and distinguished from Melaleuca moorland, than if the two moorlands were grouped within one unit and distinguished from Bulli woodland.

Nonetheless, classifications and maps will remain principal tools for conservation planning. They offer an essential means of simplifying complex spatial patterns in biodiversity and the conservation of species assemblages is a recognized goal in itself (WRI, IUCN and UNEP, 1992). It is the techniques of classification and mapping (intuitive cf. quantitative methods) and the scale of application that require more attention than previously received in conservation planning exercises. The example examined here is extreme because of the large distance between study sites, but it raises a broader question about the nature of heterogeneity in broad-scale classification units. What is the relationship between heterogeneity and distance between stands?

The extent to which heterogeneity is predictable through spatial autocorrelation remains a crucial issue that requires resolution (Sokal and Oden, 1978). If distance relationships account for much of the heterogeneity in broad-scale classification units, then conservation planning strategies would be more likely to achieve their goals if they incorporated some form of regional partitioning to ensure that units were represented throughout their distributional range (e.g. Hickey and Brown, 1989; Brown and Hickey, 1990). If heterogeneity within broad-scale classification units is mostly independent of distance, their usefulness in conservation planning may be very limited and efforts would be focussed more productively at finer scales in smaller regions. New statistical methods in spatial autocorrelation offer a means to achieve greater understanding of heterogeneity in ecosystems and its effect on widely used tools for conservation planning (Legendre and Fortin, 1989).

ACKNOWLEDGEMENTS

Belinda Pellow assisted with fieldwork at Bulli and Melaleuca. George Williams and Denny King shared their local bush knowledge of Bulli and Melaleuca moorlands, respectively. Denny King loaned us his dinghy to explore country surrounding Melaleuca Lagoon. The Sydney Water Board and Tasmanian Department of Parks, Wildlife and Heritage gave permission to work on lands under their control. Fieldwork in Tasmania was funded by the Wilderness Ecosystem Baseline Studies program. Michael Bedward and Bob Pressey gave helpful comments on a draft manuscript.

References

- AUSTIN, M.P., CUNNINGHAM, R.B., and GOOD, R.B., 1983. Altitudinal distribution of several eucalypt species in relation to other environmental factors in southern New South Wales. Australian Journal of Ecology 8: 169-180.
- AUSTIN, M. P., and MARGULES, C. R., 1986. Assessing representativeness. In USHER, M. B., (ed.), Wildlife Conservation Evaluation, pp45-67. Chapman and Hall, London.
- BARLOW, B. A., 1981. The Australian flora: its origin and evolution. *Flora of Australia* 1: 25-75. BAUR, G. N., 1988. *Forest types of New South Wales*. Research Note No. 17. Forestry Commission of New South Wales, Sydney.
- BEADLE, N. C. W., 1981. The vegetation of Australia. Cambridge University Press, Melbourne.
- BEARD, J. S., and WEBB, M. J., 1974. The vegetation survey of Western Australia: its aims, objects and methods. Great Sandy Desert. Part I of explanatory notes to Sheet 2. Vegetation survey of Western Australia, 1:1,000,000 vegetation

SIMILARITY OF SEPARATED MOORLAND VEGETATION

series. University of Western Australia Press, Nedlands.

- BEDWARD, M., KEITH, D. A., and PRESSEY, R. L., 1992. Homogeneity analysis: assessing the utility of classifications and maps of natural resources. Australian Journal of Ecology 17: 133-139.
- BELBIN, L., 1986. PATN: Pattern analysis package. CSIRO, Canberra.
- BENSON, J. S., 1989. Establishing priorities for the conservation of rare or threatened plants and plant associations in New South Wales. In HICKS, M., and EISER, P., (eds.) The Conservation of Threatened Species and their Habitats, pp17-82. Australian Committee for IUCN, Canberra.
- BOWMAN, D. M. J. S., MACLEAN, A. R. and CROWDEN, R. K., 1986. Vegetation-soil relations in the lowlands of southwest Tasmania. Australian Journal of Ecology 11: 141-153.
- BROWN, M. J., and HICKEY, J. E., 1990. Tasmanian forest-genes or wilderness? Search 21: 86-87.
- BROWN, M. J. and PODGER, F. D., 1982. Floristics and fire regimes of a vegetation sequence from sedgeland-heath to rainforest at Bathurst Harbour, Tasmania. *Australian Journal of Botany* 30: 659-676.
- BURGMAN, M. A., 1988. Spatial analysis of vegetation patterns in southern Western Australia: implications for reserve design. Australian Journal of Ecology 13: 415-429.
- CARNAHAN, J. A., 1976. Natural vegetation. Map (1:6,000,000) and commentary. In: PLUMB, T. W. (ed.), Atlas of Australian resources. Department of Natural Resources, Canberra.
- CONNELL, J. H., 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: CODY, M. L., and DIAMOND, J. M. (eds.), Ecology and evolution of communities. Belknap Press, Harvard University Press, Cambridge.
- DAVIS, C., 1940. Preliminary survey of the vegetation near New Harbour, south-west Tasmania. Papers and Proceedings of the Royal Society of Tasmania 40: 1-9.
- DAVIS, C., 1941. Plant ecology of the Bulli district II: plant communities of the plateau and scarp. Proceedings of the Linnean Society of New South Wales 66: 1-19.
- FAITH, D. P., BELBIN L., and MINCHIN, P. R., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57-66.
- HAMERICK, J. L., 1983. The distribution of genetic variation within and between populations. In: SCHOENEWALD, C. M., CHAMBERS, S. M., MACBRYDE, B., and THOMAS, W. L. (eds.), Genetics and conservation. Benjamin/Cummings, London.
- HICKEY, J.E. and BROWN, M. J., 1989. Planning for regional biological conservation of Tasmania's forest vegetation types. Proceedings of the International Foresters Association Conference, Leura.
- HUTCHINSON, G. E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *American Naturalist* 93: 145-149.
- JACKSON, W. D., 1968. Fire, air, water and earth an elemental ecology of Tasmania. Proceedings of the Ecological Society of Australia 3: 9-16.
- JARMAN, S. J., KANTVILAS, G., and BROWN, M. J., 1988. Buttongrass moorland in Tasmania. Research Report No.2. Tasmanian Forest Research Council, Hobart.
- KEITH, D. A., 1991. Coexistence and species diversity of upland swamp vegetation: The roles of an environmental gradient and recurring fires. PhD thesis, University of Sydney.
- KEITH, D. A., 1994a. Floristics, structure and diversity of natural vegetation in the O'Hares Creek catchment, south of Sydney. *Cunninghamia* 3: 543-594.
- KEITH, D. A., 1994b. Mosaics in Sydney heathland vegetation: the roles of fire, competition and soils. Calmscience Supplement 4: 199-206.
- KEITH, D. A., and BRADSTOCK, R. A., 1994. Fire and competition in Australian heath: a conceptual model and field investigations. *Journal of Vegetation Science* 5: 347-354.
- KEITH, D. A., and MYERSCOUGH, P. J., 1993. Floristics and soil relations of upland swamp vegetation near Sydney. Australian Journal of Ecology 18: 325-344.
- KEITH, D. A., and PELLOW, B. J., 1989. Temperate moorland vegetation: a comparative study of Tasmania and the Australian mainland. Unpublished report to the Department of Parks, Wildlife and Heritage, Hobart.
- KIRKPATRICK, J. B. and DICKINSON, K. J. M., 1983. Vegetation map of Tasmania, 1:500,000. Forestry Commission of Tasmania, Hobart.
- KUCHLER, A. W., 1964. Potential natural vegetation of the Conterminous United States. Map (1:3,168,000) and manual. Special Publication No. 36, American Geographic Society, New York.
- LEGENDRE, P., and FORTIN, M., 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107-138.
- MCCULLAGH, P., and NELDER, J. A., 1983. Generalised linear models. Chapman and Hall, London.
- Minchin, P. R., 1990. DECODA. ANUTECH, Canberra.
- PICKARD, J., and NORRIS, E.H., 1994. Vegetation of north-western New South Wales. Cunninghamia 3: 423-464
- PRESSEY, R. L., and BEDWARD, M., 1991. Mapping the environment at different scales: benefits and costs for nature conservation. In: MARGULES, C. R., and Austin, M. P. (eds.), Nature conservation: cost effective biological surveys and data analysis. CSIRO, Melbourne.
- RESOURCE ASSESSMENT COMMISSION, 1992. A survey of Australia's forest resource. Australian Government Publishing Service, Canberra.
- SIDDIQI, M.Y., CAROLIN, R. C., and MYERSCOUGH, P. J., 1976a. Studies in the ecology of coastal heath in New South Wales III. Regrowth of vegetation after fire. Proceedings of the Linnean Society of New South Wales 101: 53-63.
- SIDDIQI, M Y., CAROLIN, R. C., and MYERSCOUGH, P. J., 1976b. Studies in the ecology of coastal heath in New South Wales IV. Seed survival, germination, seedling establishment and early growth in *Banksia serratifolia Salisb.*, *B. asplenifolia Salisb.* and *B. ericifolia* L.f. in relation to fire: temperature and nutritional effects. *Australian Journal of Ecology* 1: 175-183.
- SNEDECOR, G. W., and COCHRAN, W. G., 1963. Statistical methods. Iowa State University Press, Ames.
- SOCHAVA, V. B., and LUKICHEVA A, N., 1964 Vegetation of the U. S. S. R. map (1:15,000,000) and text. In:

GERASIMOV, I. P. et al. (eds.), Fiziko-geografischeskii Atlas Mira, plates 240-1, pp. 280-3. Academy of Sciences of the U.S.S.R., Moscow.

- SOKAL, R. R., and ODEN, N. L., 1978. Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest. Biological Journal of the Linnean Society 10: 229-249.
- SPECHT, R. L., ROE, E. M, and BOUGHTON, V. H., 1974. Conservation of major plant communities in Australia and Papua New Guinea. Australian Journal of Botany. Supplementary Series No. 7.

- TILMAN, D., 1982. Resource competition and community structure. Princeton University Press, Princeton. WHITE, F., 1983. The vegetation of Africa: a descriptive memoir to accompany the UNESCO/AESTAT NUSO vegetation map (1:5,000,000) of Africa. UNESCO, Paris.
- WRI, IUCN and UNEP, 1992. Global biodiversity strategy. Guidelines for action to save, study and use earth's biotic wealth sustainably and equitably. World Resources Institute, World Conservation Union and United Nations Environment Program.